

Neural activity in the visual thalamus reflects perceptual suppression

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To examine the role of the visual thalamus in perception, we recorded neural activity in the lateral geniculate nucleus (LGN) and pulvinar of 2 macaque monkeys during a visual illusion that induced the intermittent perceptual suppression of a bright luminance patch. Neural responses were sorted on the basis of the trial-to-trial visibility of the stimulus, as reported by the animals. We found that neurons in the dorsal and ventral pulvinar, but not the LGN, showed changes in spiking rate according to stimulus visibility. Passive viewing control sessions showed such modulation to be independent of the monkeys' active report. Perceptual suppression was also accompanied by a marked drop in low-frequency power (9–30 Hz) of the local field potential (LFP) throughout the visual thalamus, but this modulation was not observed during passive viewing. Our findings demonstrate that visual responses of pulvinar neurons reflect the perceptual awareness of a stimulus, while those of LGN neurons do not.

vision | LGN | awareness | pulvinar | attention

Studies of the neural mechanisms of visual perception frequently rely on illusions that dissociate the contents of perception from retinal stimulation. During the phenomenon of perceptual suppression, for example, a salient visual stimulus can be made to subjectively disappear while attention is directed to it (1–3). Perceptual suppression paradigms have been used in human and nonhuman primates and have revealed perceptual correlates in many cortical areas, with some discrepancy between neurophysiological and functional magnetic resonance imaging (fMRI) studies concerning the role of early visual areas (4–12).

The present study explores perceptual visibility correlates in the visual thalamus, whose major elements in the primate consist of the lateral geniculate nucleus (LGN) and the pulvinar. The LGN is the primary relay of visual information from the retina to the cerebral cortex. Whereas its driving input comes from retinal ganglion cells, it also receives modulating inputs from extraretinal sources, including the cortex (13, 14). By contrast, the adjacent pulvinar nucleus is a complex structure that receives its main driving input from the cerebral cortex (15–17). Its subregions are reciprocally connected to specific cortical areas, including the striate and extrastriate visual cortex (18). Following previous conventions (19, 20), we conceptually divide the pulvinar into a ventral and a dorsal part. Its ventral aspect (corresponding to the traditionally defined inferior pulvinar and ventral portion of the lateral pulvinar) receives input from the visual cortex and from superficial layers of the superior colliculus (SC). Its dorsal aspect (corresponding to the medial pulvinar and dorsal portion of the lateral pulvinar) receives input from extrastriate visual areas, posterior parietal and frontal cortex, multisensory areas in the superior temporal sulcus, and intermediate and deeper layers of the SC (17–19).

On the basis of the strong corticofugal input to the visual thalamus, there is reason to believe that responses of neurons there would be shaped by cognitive factors having their origins in the cortex. One such factor is spatial attention, which is thought to selectively gate visual information. Indeed, previous electrophysiological studies have shown that neurons in the pulvinar (21–23)

and in the LGN (24, 25) are modulated by attention, with human imaging studies demonstrating attentional modulation of the blood-oxygen-level-dependent (BOLD) signal in both nuclei (26–29). Another cognitive variable, whose relationship to spatial attention is complex, is the perceptual awareness of a stimulus. While suppression paradigms have been used extensively to investigate perceptual activity of cortical neurons, relatively little work has been directed toward neurons in the visual thalamus. Would cells in the LGN and pulvinar alter their firing rates according to whether a physical stimulus is perceptually visible? The most relevant neurophysiological study examined the responses of LGN neurons during binocular rivalry in awake monkeys. That study found no evidence for perceptual modulation (30), although this finding must be interpreted with caution since monkeys did not actively report their percepts. In contrast, recent human fMRI studies found strong BOLD signal modulation in the LGN associated with periods of perceptual dominance and suppression during binocular rivalry (31, 32).

Although there is some evidence from human fMRI studies that the pulvinar is involved in visual perception (33–35), neither fMRI nor electrophysiological studies investigating neural correlates of perceptual suppression have reported on activity changes in the pulvinar (36, 37).

Perhaps the best evidence for a direct role of the pulvinar in visual awareness comes from neuropsychological studies, in which pulvinar damage has been associated with visual neglect and feature-binding deficits (38–40).

The present study used the paradigm of generalized flash suppression (GFS) (2) to dissociate physical stimulation from perceptual experience. This approach has previously been used to investigate perceptual correlates in the visual cortex and revealed that neurons in extrastriate, but not striate, visual areas were significantly influenced by the visibility of a stimulus (9, 41). In the present study we recorded neuronal spiking activity along with field potentials in the visual thalamus while trained monkeys actively reported their percepts. We found that whereas spike rates of LGN neurons were unaffected by perceptual suppression, those within the pulvinar were significantly modulated according to the perceptual state. In addition, low-frequency local field potential (LFP) power (9–30 Hz) decreased in both nuclei during perceptual suppression, although this latter effect was contingent upon the monkey's active report. Our results demonstrate that responses of neurons in the pulvinar, but not the LGN, reflect the subjective visibility of a stimulus.

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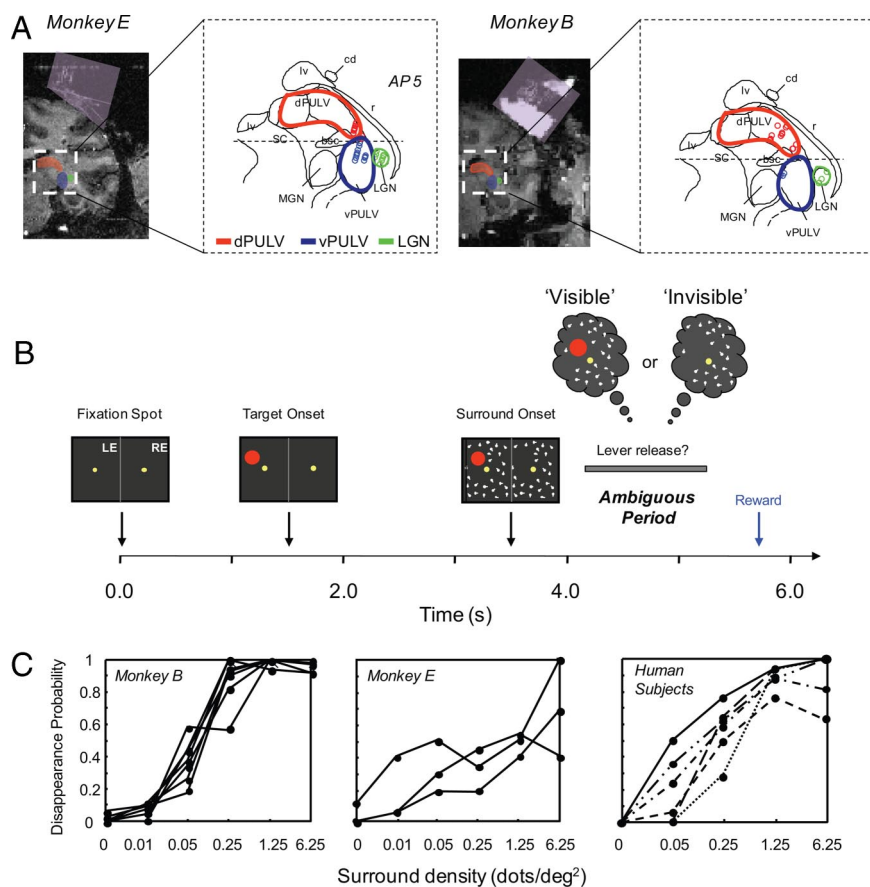


Fig. 1. MRI of recording chamber and recording sites mapped onto monkey brain atlas(53). (A) Coronal MRI slice showing chamber position of monkey E and B and reconstructed location of recording sites (colored dots, estimated AP + 5): LGN (green), vPULV (blue), and dPULV (red), projected on an outline modified after the monkey atlas (53). A complete reconstruction of recorded sites is depicted in Fig. S1 and criteria are explained in SI Methods. vPULV, ventral pulvinar; dPULV, dorsal pulvinar; LGN, lateral geniculate nucleus; bsc, brachium of the superior colliculus; R, reticular nucleus, cd, caudate nucleus; lv, lateral ventricle. (B) Illustration of a (perceptually ambiguous) test trial. Monkeys were required to fixate a central spot for 1,500 ms before the target stimulus (red disk) appeared at a parafoveal position. The target was presented for 2,000 ms before the surround pattern, consisting of randomly moving dots, was added to the presentation. Monkeys were required to pull a lever as long as the target was visible. If the target became invisible, either because of perceptual suppression or its physical removal, monkeys had to release the lever within 800 ms and keep fixating for another 800 ms to receive a juice reward. LE, left eye; RE, right eye. (C) Psychophysical results during individual sessions obtained for monkey and human observers. Probability of target disappearance during test trials as a function of surround density for monkey B (7 sessions) and monkey E (3 sessions) and 6 human observers (single session data, from ref 2). Each point corresponds to the probability of reported target disappearance within the first 1,200 ms after surround onset. Note that both monkeys and humans reported increased target suppression rates with increasing surround densities, indicating that GFS was effective in these monkeys.

Results

In 2 trained macaque monkeys, we performed 113 sessions, recording LFP and spiking activity from a total of 177 visually responsive sites while monkeys reported their percepts: 68 in the dorsal pulvinar (dPULV), 63 in the ventral pulvinar (vPULV), and 46 in the LGN (see Fig. 1, *Materials and Methods*, Table S1, and SI Methods). Neurons were recorded throughout the posterior aspect of the LGN. While our testing did not permit a thorough analysis of all physiological properties, the majority of sites showed sustained neural responses and were recorded from the posterior/dorsal portion of the LGN (Figs. S1 and S2) and were therefore most likely in the parvocellular layers. For the present study, modulation of the tonically firing parvocellular neurons was of particular interest, given the prolonged nature of perceptual suppression.

Behavioral Paradigm and Psychophysical Results. Monkeys were trained to report the visibility of a high-contrast target in the context of GFS (2). Briefly, GFS is a stimulation sequence in which the subjective disappearance of a salient target stimulus (red disk in Fig. 1B) is induced by the abrupt appearance of moving random dots in surrounding regions at some distance from the target. The spatial requirements of GFS are similar to those of motion-induced blindness (1), whereas its temporal dynamics resemble those of binocular rivalry flash suppression (3) and thereby afford good experimental control over the timing of the perceptual states. Psychophysical experiments in humans have shown that suppression during GFS is characterized by complete disappearance of the target, occurs while the target is attended, is sustained for up to several seconds, and is particularly effective when the target and surround are shown to different eyes (2). As described previously, adjusting stimulus parameters such as the eye assignments of target

and surround stimuli, or the density of the surround dots, makes it possible to systematically vary the probability of target suppression (2, 9, 41). Such parametric manipulations are essential in nonhuman primate experiments because they allow for both *unambiguous* stimulation (where the experimenter has complete control over target disappearance—0% or 100%) and *ambiguous* stimulation (where the target has roughly the same probability of disappearing as not disappearing—50%). The former constitutes the behavioral training and control (“catch”) trials, while the latter represents the experimental trials, where target visibility is sorted on the basis of the monkey’s responses. The GFS trial structure, outlined in Fig. 1B, started with target presentation for 2 seconds, followed by the addition of a nonoverlapping pattern of randomly moving dots surrounding the target. Monkeys were initially trained to report target visibility by holding a lever whenever the target was presented during unambiguous stimulation and releasing it when the target was physically removed from the screen (henceforth “control”) (see SI Methods).

For the experimental trials, the stimulus parameters were adjusted for each session to achieve disappearance in $\approx 50\%$ of the test trials. Psychophysical adjustments were made after positioning the target in the receptive field (RF) of the recorded cells. Fig. 1C shows the effect of varying the dot density for the 2 monkeys and for several humans (2). Accuracy of the monkeys’ reports was continually enforced and validated during electrophysiological testing by interleaving a relatively small number of perceptually ambiguous test trials with a much larger fraction of unambiguous control trials (see *Materials and Methods*).

Neurons in Pulvinar, but Not LGN, Affected by Perceptual Suppression. Fig. 2A shows responses from a neuron recorded in the dPULV. Following the onset of the surround stimulus, the visibility of the target had a strong impact on this neuron’s firing, even though the

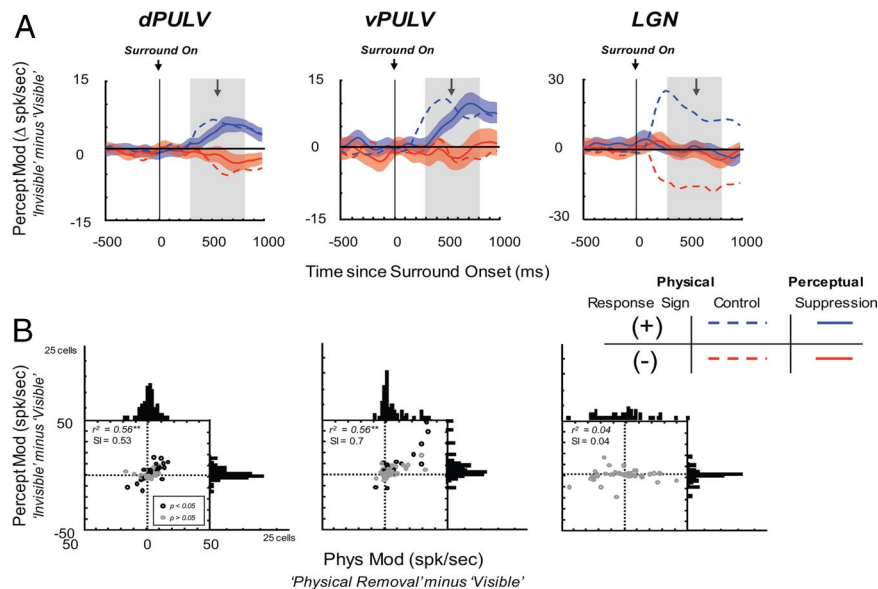


Fig. 3. Population modulation of spiking responses during perceptual suppression. (A) Plots show the mean differential time courses between the “invisible” and “visible” condition induced by physical removal (i.e., control condition, dashed lines) and perceptual suppression condition (i.e., test condition, solid lines) for dPULV, vPULV, and LGN. Modulation because of the physical removal or perceptual invisibility of the stimulus is indicated by deviations from zero over time. Because of the heterogeneous responses of neurons, data were separated into 2 groups on the basis of sign of activity change in the physical removal control. Grand (difference) mean of spiking responses in dPULV and vPULV for all target responsive sites showing an activity increase when the target was physically removed from the screen at surround onset (blue: dPULV, $n = 41$; vPULV, 46; LGN, $n = 16$) and neurons showing an activity decrease upon physical target removal (orange: dPULV, $n = 27$; vPULV, 17; LGN, 30). Shaded areas represent the continuous standard error of the mean between recording sites (± 1 SEM). Note the activity difference between the 2 visibility states in dorsal and ventral pulvinar portions and its absence in LGN. (B) Scatterplots for all target responsive sites in pulvinar and LGN. Plots compare spike-rate modulations following physical target removal (x axis) and perceptual target disappearance (y axis) (mean over 300 to 800 ms after surround onset), dPULV ($n = 68$), vPULV ($n = 63$), and LGN ($n = 46$). Black circles indicate sites with significant perceptual modulation (2-sample t test over trials, $P < 0.05$). Histograms show distribution of physical removal differences (Top) and perceptual suppression differences (Right). Note the strong correlation between strength of the modulation because of physical removal and that of perceptual suppression in dPULV and vPULV and its absence in the LGN.

30–50 Hz) in any of the structures, power in the higher gamma range (γ_{high} , 50–80 Hz) was modestly but significantly increased in the pulvinar, matching the physical removal condition (2-tailed t tests over all sites in each structure, see also Fig. S7 and S8).

Finally, in contrast to the spiking results collected from the same electrodes, perceptual modulation in the LFP disappeared entirely during the passive viewing condition (Fig. 4B). The selective absence of visibility-related BLP activity during passive viewing indicates that the LFP modulation reflected some element of the task structure, rather than the perception of the stimulus itself. The particular aspect of the task that caused the robust low-frequency modulation during the active condition, may be related to the role

of the pulvinar in attention, decision-making, or behavioral planning, and is outside the scope of the present study.

Discussion

The primate pulvinar is widely regarded as a visual structure, on the basis of the abundant connections with the visual cortex and the existence of retinotopic maps in its ventral aspect (18, 42, 43). Our findings indicate that these visual responses are nearly as closely related to the perception of a visual stimulus as to its physical presence on the retina. In fact, perceptual modulation in the pulvinar was more prevalent and proportionally stronger than that previously observed in the striate and extrastriate

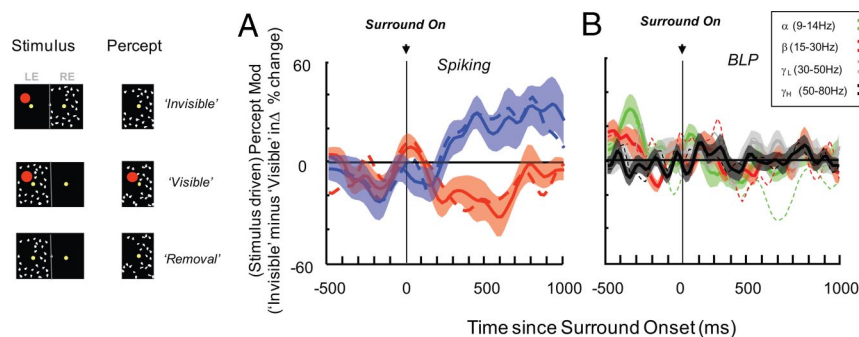


Fig. 4. Perceptual modulation under passive viewing conditions. Perceptual suppression was induced by the stimulation itself and monkeys did not report. Following 2,000 ms of target presentation, the spatially nonoverlapping surround was added either to the same eye (“visible”) or to the opposite eye (“invisible”). (A) Population activity ($n = 18$). Grand (difference) mean of spiking responses (analogous to Fig. 3A) in dPULV/vPULV for all target responsive sites showing an activity increase when the target was physically removed from the screen at surround onset (blue: $n = 15$) and neurons with an activity decrease upon physical target removal (i.e., control condition, orange: $n = 3$). Note the significant activity differences between the 2 (presumed) visibility states in the spiking activity under those passive viewing conditions. (B) Differential mean in the local field potential power for each region (analogous to Fig. 2B). Different colors indicate frequency bands (legend).

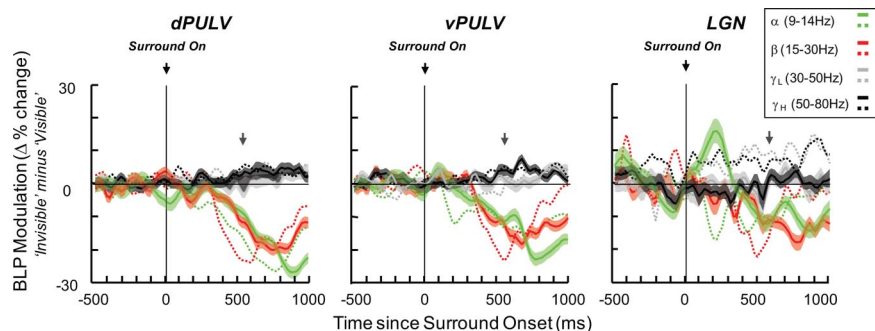


Fig. 5. Perceptual modulation as a function of frequency band in the local field potential power. Plots show the mean *differential* responses between the physical removal (i.e., control condition, ["removal" minus "visible"], dashed lines) and perceptual suppression condition (i.e., test condition, ["invisible" minus "visible"], solid lines) (dPULV, $n = 68$; vPULV, 63; LGN, $n = 46$). Modulation to the physical removal or perceptual invisibility of the stimulus is indicated by deviations from zero over time. Different colors indicate frequency bands (legend). Shaded areas of the same color represent the continuous standard error of the mean between recording sites (± 1 SEM). Note the overall decrease of low-frequency power during perceptual suppression in dPULV, vPULV, and LGN.

visual cortex (V1, V2, and V4) using the same method (41). We found a diversity of neural responses during perceptual suppression, with some cells showing excitatory and others inhibitory spiking modulation, typically related to the physical target on- and offset responses. This mixture of response types may reflect the role of the pulvinar as a convergence point of sensory signals from the visual cortex and abundant input from cortical areas concerned with transforming visual information into behavioral events.

Indeed, previous studies in monkeys have shown that lesioning or inactivating the pulvinar does not lead to the same visual deficits observed following similar manipulations to the LGN or primary visual cortex. Rather than giving rise to deficits in stimulus detection, pattern discrimination, or visual search, pulvinar damage typically gives rise to higher-level impairments in attentional selection (23, 44–47). In addition, lesion studies in humans have identified pulvinar-related deficits of spatial localization, feature and temporal binding (39, 48), and visual awareness (38).

Cells in the LGN, by contrast, appeared to be driven exclusively by the physical stimulus. Because most cells were recorded from the parvocellular layers, we cannot exclude the possibility of suppression-related activity in the magnocellular layers. However, the lack of visibility-related spiking activity in the LGN is consistent with an earlier electrophysiological study that investigated spike rate modulations in both layer types in the context of binocular rivalry (30). This lack of perceptual activity is puzzling in the light of BOLD response modulation observed there during binocular rivalry in humans (31, 32). The substantial decrease in LFP observed during perceptual suppression might suggest the reported BOLD responses reflect subthreshold extraretinal inputs, which are not driving neuronal spiking rates but exert their effects on a subthreshold level (13, 49). Another possibility is that the LFP modulation measured in the LGN is unrelated to its local neural activity, instead reflecting the volume conduction of signals originating elsewhere (e.g., the pulvinar).

Contribution of Attention. The complex relationship between attention and perception cannot be easily summarized. Recent experiments have demonstrated that these cognitive variables can, at least to some extent, be treated as distinct entities (50). The GFS paradigm has advantages and disadvantages with respect to dissociating perceptual from attentional modulation. One advantage lies in the fact that during the perceptual report, the animal must continually attend to the location of the target to make correct responses. While this method does not prevent the animal from dividing spatial attention to some extent, it ensures through reward contingencies and catch trials that that point in space is attended, whether the target is perceptually visible or invisible. A disadvan-

tage of the GFS paradigm lies in its asymmetrical nature. A perceptual transient associated with target disappearance may attract exogenous attention. We cannot entirely exclude the possibility that the perceptual modulation in the pulvinar is secondary to an attentional shift. However, it is important to point out that if an exogenous shift of attention were responsible for the observed spiking modulation in the pulvinar, it would need to have the following properties. First, it would have to be sustained, because the modulation we observed lasted at least several hundreds of milliseconds. Second, the exogenous shift would need to be sensitive to a *perceptual* (rather than sensory) cue, because the sensory stimulus is the same in both visible and invisible trials. Finally, the attention must not be tightly linked to the task structure, because diminishing the behavioral relevance of the target in the passive fixation condition did not abolish visibility-related spiking modulation in the pulvinar. Thus while we cannot fully exclude any contribution of attention, we believe perceptual modulation, based on stimulus visibility, offers the most parsimonious explanation for the observed spiking rate changes. The animal's attentional disposition may be more directly reflected in the LFP signal, for which modulation depended on the task demands, an interpretation consistent with a recent study conducted in cats (51).

In summary, our findings, taken together with other observations such as visual neglect following pulvinar lesions, indicate that visual responses of neurons in the primate pulvinar reflect the perceived contents of a scene.

Materials and Methods

Data Acquisition. Two adult *Macaca mulatta* monkeys [Elvis (E) and Barney (B)] participated in the study. Monkeys participated for a total of 113 recording sessions (62 Elvis, 51 Barney; see Table S1). Data were recorded while the animals reported target visibility in the context of GFS while maintaining fixation. We recorded with 4 to 8 microelectrodes simultaneously (Thomas Recording GmbH). Spiking and local field potential activity was collected with the MAP recording system (Plexon). All experimental protocols were conducted following National Institutes of Health guidelines. Results from the 2 animals were similar and are, unless otherwise mentioned, considered together. Detailed descriptions of behavioral task, training, and data acquisition are available in *SI Methods*.

Stimuli and Behavioral Task. Perceptual suppression was induced using the GFS paradigm, which has been described in detail previously (2, 41). In the current study, the target stimulus (luminance patch or grating) was presented for 2 seconds followed by the onset of moving, nonoverlapping dots (2). Target eccentricity was varied on the basis of the position of the RF of recorded neurons (target eccentricities: 0.4° to 7.7°). For a given RF eccentricity, target size (0.3° to 6.0°) and target edge-surround distance (0.5° to 4.0°) were optimized for a given session to achieve target disappearance in about 50% of the test trials. An example stimulus sequence is shown in Fig. 1B. The behavioral control trials were designed to unambiguously present the monkey with either a visible or invisible target. To achieve this, stimuli were adjusted such that the surround onset would

itself not cause perceptual target disappearance, and the physical disappearance was controlled by the experimenter. For these trials, the target and surround were presented to the same eyes (monocularly or binocularly). The target was then removed either immediately (after 80 ms) following the surround onset or it remained present (and visible) much longer (up to 6,000 ms). These control trials, which far outnumbered the test trials (on average 4:1), ensured that the animals would hold and release the lever according to the perceived visibility of the target. In perceptually ambiguous test trials the target and surround pattern were presented to opposite eyes. During test trials, monkeys were permitted to release the lever any time after the onset of the surround. The passive viewing task is described in *SI Methods*.

Stimuli were displayed on 38×65 -cm monitors through a mirror stereoscope. The eye-screen distance was 88 cm. During trials, a blue fixation spot (0.15°) was always presented in the middle of the screen and monkeys were required to maintain fixation within a 0.7° radius.

Data Analysis. Neurophysiological data were processed and analyzed offline using custom-written software in MATLAB. Spiking data were converted into histograms using a bin width of 25 ms. Target onset responses were assessed over a time window (50–500 ms) after target appearance, in comparison to the preceding fixation baseline (500 to 0 ms). LFP data were subdivided into different frequency bands using a second-order, bidirectional, zero-phase Chebyshev type-1 filter and full-wave rectified (see *SI Methods* and ref. 52 for a detailed description). Signals obtained during test trials were categorized offline as either visible or invisible, on the basis of the monkey report. Trials were classified as

visible when the monkey continued to hold the lever for more than 2,000 ms following surround onset and were classified as invisible when the monkey released the lever within 800 ms following surround onset. Perceptual modulation is defined as the activity difference between those visible and invisible trials ([invisible minus visible]) as reported by the monkey for structurally identical test trials. Physical modulation was analogously computed as the difference between trials where the target remained visible and trials where the target was physically removed ([physical removal minus visible]). In contrast to the pulvinar, neurons in the LGN have strong ocular preferences and respond almost exclusively to a target presented to 1 of the 2 eyes. For the analysis of LGN sites, we therefore considered only trials where the target was presented to the dominant eye. Band-limited power signals on a given channel are expressed in percent change with respect to the baseline activity during the fixation period (baseline defined as time period between 500 and 0 ms before target onset) $\% \text{ signal}(t) = ((\text{signal}(t) - \text{signal}(\text{baseline})) / \text{signal}(\text{baseline})) \times 100$.

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